Diet of Juvenile and Adult Atlantic Menhaden in Estuarine and Coastal Habitats

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Abstract.—The Atlantic menhaden *Brevoortia tyrannus* is a pelagic, obligate filter-feeding fish. Although much of the primary literature indicates that amorphous matter is a major component of the stomach contents of Atlantic menhaden, the diet of these fish is typically perceived to consist primarily of phytoplankton and zooplankton. This disparity between observation and perception results from the belief that amorphous matter in the stomachs is the remnants of plankton that were ingested alive or that it is detritus of low nutritional value and only incidentally ingested. In this study, we found that the stomach contents of juvenile and adult Atlantic menhaden in estuarine creeks were 81% amorphous matter, 17% phytoplankton, and 1% zooplankton, by dry weight. Sampling in two estuarine creeks in North Carolina revealed no seasonal change in diet. Stomachs of fish collected from coastal waters contained smaller amounts of amorphous matter (47%) and higher amounts of phytoplankton (36%) and zooplankton (18%) than stomachs of fish from estuarine creeks. The higher concentration of plankton in the diet of fish in coastal locations probably reflects the lower concentration of suspended amorphous matter and higher relative abundance of plankton typical of that environment. In stomachs that contained largely amorphous matter, the concentrations of ash (70%, dry weight) and humic compounds (38%, ash-free dry weight [AFDW]) were high and the carbohydrate content was moderately low (14%, AFDW). On the basis of reported concentrations of these compounds in plankton and amorphous aggregates, we conclude that the amorphous matter we found in the stomachs of Atlantic menhaden was not recently ingested living or moribund plankton, but was probably material that was produced in the environment by the aggregation of dissolved organics from various detrital sources, including decaying vascular plants. If vascular plants contribute to the production of amorphous matter, their role in coastal and estuarine energy flow and fishery production may be underestimated.

Atlantic menhaden *Brevoortia tyrannus* are abundant in the coastal waters of the eastern United States and are of considerable commercial and ecological importance. However, reassessment of their ecological role may be appropriate because the importance of amorphous matter in their diet is uncertain. Juvenile and adult Atlantic menhaden feed exclusively by filtering small particles from the water (June and Carlson 1971; Durbin and Durbin 1975; Friedland et al. 1989). These particles range in diameter from 2 μm (personal observation) to 1,200 μm (Durbin and Durbin 1975), and include phytoplankton, zooplankton, and aggregations of amorphous matter. A more accurate assessment of the relative importance of these items in the diet would contribute greatly to our understanding of the trophic role of Atlantic menhaden (Peters and Schaaf 1991).

Most of the primary literature that describes the diet of Atlantic menhaden and the closely related species, the gulf menhaden *Brevoortia patronus,* indicates that large amounts of amorphous matter (also variously identified as oozy mud, greenish or brownish mud, organic detritus, unidentifiable organic matter, amorphous detritus, and detritus) are present in the stomachs of these fish. Of twelve such reports (i.e., Verrill 1871; Goode 1879; Peck 1894; Richards 1963; Darnell 1958, 1964; Mulkana 1966; June and Carlson 1971; Jeffries 1975; Peters and Kjelson 1975; Edgar and Hoff 1976; Lewis and Peters 1984), only one (Richards 1963) did not mention the presence of amorphous matter in the stomachs. Three of those studies (Peck 1894; Mulkana 1966; June and Carlson 1971) seemed to emphasize the importance of living plants and animals in the diet of Atlantic menhaden. This tendency to underemphasize or ignore the role of amorphous matter is even more dramatic in the secondary literature (e.g., Bigelow and Schroeder 1953; Reintjes 1969; Manooch 1984; Stickney 1984) and is probably based on the assumption that amorphous matter is either ruptured plankton or detritus with little nutritional value. However, neither assumption is adequately supported by scientific evidence.

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In this paper, we describe the diet of Atlantic menhaden throughout their geographic range and present evidence of diet differences between fish in estuarine and in coastal habitats. We also describe the carbohydrate, humic compound, and ash content of samples from stomachs containing mostly amorphous matter, and we evaluate the possibility that it was ingested primarily as amorphous matter rather than as living or moribund planktonic organisms. "Amorphous matter," as we use the term in the rest of this paper, denotes the nonparticulate aggregate of organic matter that we found in the stomachs of Atlantic menhaden. It resembles, and may be identical to, the amorphous matter that occurs in the environment and is formed by the aggregation of organic precipitates, as described by Bowen (1984, 1987).

Methods

Sampling design. — We examined the stomach contents of juvenile and adult Atlantic menhaden from estuarine and coastal habitats along the eastern coast of the United States in 1985 and 1986. Samples were taken to enable us to describe the diets of Atlantic menhaden in estuarine and coastal habitats over their latitudinal range and throughout their seasonal occurrence in estuarine creeks. Schools of Atlantic menhaden in estuarine creeks were sampled by cast net; samples from coastal habitats were taken from commercial purse-seine catches.

Twenty samples were collected from estuarine creeks from May to early August 1985 and 1986. These samples were processed to provide a taxonomic description of diet based on visual analysis of stomach contents of a single fish from each sample and based on chemical analysis of the pooled stomach contents of 3–50 fish from the same sample. Eleven creeks from five geographic areas were randomly selected and sampled during the summer of 1985 (Figure 1). Nine samples were collected from creeks in four of the five geographical areas in 1986; the Chesapeake Bay region was not sampled in 1986.

We also attempted to collect fish at 3-week intervals during May–October 1986 from two tidal creeks, Broad Creek and Pungo Creek, in North Carolina. Broad Creek is small and polyhaline, and flows into Bogue Sound just west of Taylors Creek. Pungo Creek is large and mesohaline, and flows into Pamlico Sound. Fish were not always available in these creeks when we sampled, but we were able to collect five samples from Pungo Creek (May–August) and eight from Broad Creek (May–October).

We also did taxonomic and chemical analysis of six samples collected from coastal waters in the summer of 1985 (Figure 1). Sampling locations were determined by the fishing patterns of the commercial fleet.

Fish used in this study were 56–298 mm in fork length. Adults longer than 230 mm were the only fish caught in New England estuaries. Fish size was less than 170 mm in all other estuarine regions. Fish sampled from coastal habitats were longer than 170 mm.

Microscopic analysis. — Fish were placed on ice at the time of capture and the contents of the esophagus and cardiac stomach of the fish were removed within 0.5–3.0 h and stored in 5% buffered formalin. Material removed from the pyloric stomach was not used in the microscopic analysis because that section of the stomach pulverizes the ingested food, rendering particles less identifiable. Subsamples were placed in an Utermohl settling chamber (Guillard 1973) and stained with Lugol's solution. All vascular plant fragments and microzoa in the chamber were counted and their dimensions were measured at $98\times$ magnification. Because microphytes (unicellular benthic algae and phytoplankton) were smaller and more numerous, they were counted and measured in 20 randomly selected quadrats at $280\times$ magnification. Bacteria were examined separately at $1,200\times$ magnification, with the direct-count epifluorescence technique (Ferguson and Rublee 1976). Bacteria estimates were done only for the samples randomly selected in 1985.

Each discrete particle was measured under a microscope, and its volume was calculated and used to estimate its dry weight. The volume was calculated according to the geometric shape most closely approximating that of the particle: perfect spheroid, hemispheroid, prolated spheroid, oblate spheroid, cone, cylinder, or rectangular prism. To determine wet weight, a density of 1.0 g/cm^3 was assumed. To calculate dry weight from wet weight, we used the following conversion factors: microphytes, 0.30 (Strickland 1960); copepods, 0.13; invertebrate eggs, 0.10 (Vinogradov 1953); tintinnids, 0.20 (Beers and Stewart 1969); vascular plant fragments, 0.91 (Burkholder 1956); bacteria, 0.30 (Ferguson and Rublee 1976). A conversion factor of 0.20 was used for miscellaneous plankton.

The amount of amorphous matter in the stomachs was estimated as the difference between total dry weight in the stomach and the sum of the
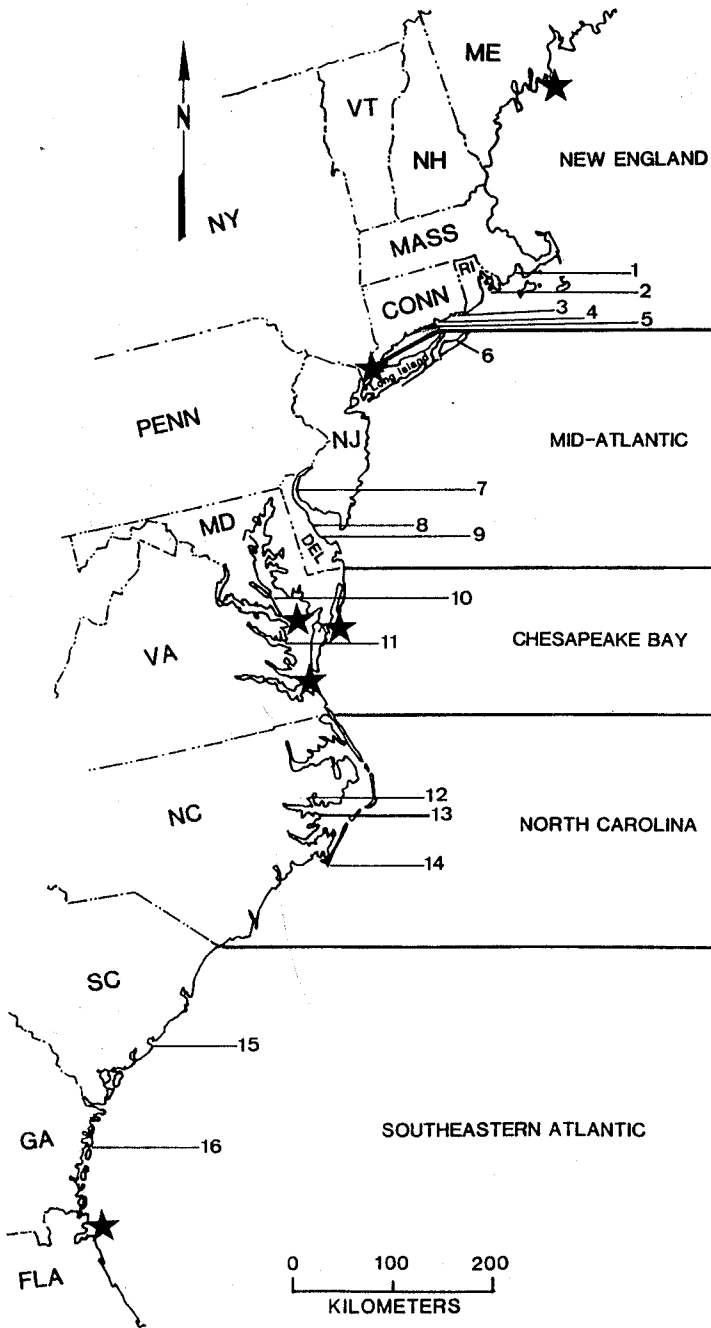
FIGURE 1.—Areas along the east coast of the United States from which Atlantic menhaden were sampled. Estuarine sampling sites are indicated by numerals: (1) Weir Creek, (2) Apponagansett Bay, (3) Hammonassett River, (4) West River, (5) East River, (6) North Sea Harbor, (7) Augustine Creek, (8) Red Lion Creek, (9) Blackbird Creek, (10) Patuxent River, (11) Rappahannock River, (12) Pungo Creek, (13) South River, (14) Taylors Creek, (15) Dawhoo River, and (16) White Chimney River. Coastal sampling sites are indicated by stars.

estimated dry weights of all other diet components. Total dry weight was determined by filtering a measured subsample through a dried, preweighed glass fiber filter and rinsing the filter with cold distilled water. The filter was then redried at 70°C for 24 h and weighed to determine the total sample weight. The dry weight of amorphous matter determined by this technique is subject to the cumulative errors of all other estimates. Because most of this material was irregularly shaped and its percent wet weight was not known, we believed that this was the best available technique for estimating its percent dry weight.

Chemical analysis. —Samples for chemical analysis were collected from the esophagus and from the cardiac and pyloric sections of the stomach. Although material in the pyloric section has been subjected to pulverization, its chemical identity should not have been altered, and therefore chemical analysis of the food probably would not be biased by its inclusion. Ingested material was stored on dry ice until it was freeze dried. Samples of at least 10 g dry weight were obtained by pooling the stomach contents of 3–50 fish from each sampling station. Dried pooled samples were ground with mortar and pestle and stored in a desiccator until chemical analysis was performed. Although mucus and digestive enzymes probably contributed to the chemical composition of ingested material, we assumed that they did not substantially bias the estimates.

Ash content was determined after incineration of a subsample in a muffle furnace for 3 h at 550°C. Total carbohydrates were determined by the phenol–sulfuric acid technique of DuBois et al. (1956), as modified by Gerchakov and Hatcher (1972). Subsamples were suspended in distilled water and ultrasonically dispersed. Aliquots of each of the subsamples were reacted with sulfuric acid in the presence of phenol and then centrifuged. Optical density was measured at 570 nm with glucose as a standard. Humic compounds (fulvic acid, humic acid, and humin) were determined following alkaline extractions of the material. Humic and fulvic acids, soluble in dilute base, were determined collectively by the chemiluminescent technique of Slawinska and Slawinska (1967), as modified by Marino and Ingle (1981). Because there is no method for the direct determination of humin in stomach samples, we determined it gravimetrically as the residual organic matter following the extraction of all soluble components. The lipid content of subsamples were extracted with 4:1 petroleum ether–ethanol solvent. Protein (including free amino acids), humic and fulvic acids, and alkali-soluble carbohydrates were extracted with alkaline solutions of 0.5 M NaOH. The subsamples were then rinsed with hot distilled water and ethanol and dried at 100°C for 3 h. Humin content was determined as the residual matter less the ash content. The humin content was combined with the fulvic and humic content to estimate total humic compounds.

Chemical analysis of amorphous matter in the stomachs was not possible because there was no way to physically separate it from the other diet components. As a proxy for the ash, carbohydrate (ash-free dry weight, AFDW), and humic compounds (AFDW) content of amorphous matter, we present the average chemical composition of samples that were mostly (>85%) amorphous matter.

Results

Microscopic Analysis

Amorphous matter was the most abundant of the stomach contents of Atlantic menhaden from estuarine creeks. By dry weight, it accounted for 80% of the material in the stomachs of fish from randomly selected creeks and accounted for 70–80% of stomach contents of fish in Broad and Pungo creeks (Table 1). Phytoplankton was moderately abundant and zooplankton was typically of low abundance. Zooplankton was substantially more abundant in fish from Broad Creek than in fish from other creeks. Bacteria and vascular plant fragments were consistently of very low abundance.

Amorphous matter and phytoplankton were major components of the diet of fish in coastal waters, but zooplankton was also moderately abundant (Table 1). Amorphous matter was the major item in stomachs of fish from three of the six locations (84, 81, and 59%), phytoplankton was dominant in stomachs of fish from two locations (80 and 57%), and zooplankton was dominant in fish from one location (86%). Bacteria were typically a minor component of the stomach contents; vascular plant fragments were virtually absent.

Chemical Analysis

Ash was about 57–70% of the dry weight of the food in the stomachs of Atlantic menhaden (Table 2). Humic compounds were about 23–38% of the AFDW and the concentration was lower in fish from coastal habitats. Carbohydrates accounted

TABLE 1.—Major components (percent dry weight) of the stomach contents of juvenile and adult Atlantic menhaden from estuarine creeks and coastal waters of the east coast of the United States, 1985–1986.

Sample area	Statistic[a]	Amorphous matter	Phytoplankton	Zooplankton	Plant fragments	Bacteria
		Randomly selected creeks				
All	Mean	80.5	17.3	1.1	0.7	0.4
	SE	3.8	3.9	0.3	0.2	0.2
	CV	21.1	99.1	101.8	136.8	150.0
	N	20	20	20	20	11
		Seasonally sampled creeks, North Carolina				
Pungo Creek	Mean	81.1	14.4	3.7	0.9	
	SE	4.3	5.4	1.1	0.5	
	CV	11.9	84.0	66.5	132.7	
	N	5	5	5	5	
Broad Creek	Mean	68.8	5.5	24.8	0.9	
	SE	5.7	1.6	16.3	0.3	
	CV	23.4	81.6	72.1	94.0	
	N	8	8	8	8	
		Coastal waters				
All	Mean	46.2	35.6	17.8	<0.1	0.4
	SE	13.6	11.2	13.7	<0.1	0.2
	CV	72.0	77.4	188.8	62.0	86.5
	N	6	6	6	6	6

[a] CV = coefficient of variation (100·SD/mean). N = number of stomachs.

for about 9–17% of the AFDW. The average content of 14 samples that contained 86–96% amorphous matter was 70% ash (dry weight), 38% humic compounds (AFDW), and 14% carbohydrates (AFDW) (Table 3).

Discussion

The diet of Atlantic menhaden determined in this study (Table 1) is similar to most of the diets reported in the primary literature for this species. The average diet from the five studies that provided quantitative estimates (Darnell 1964; Jeffries 1975; Peters and Kjelson 1975; Edgar and Hoff 1976; Lewis and Peters 1984) was 87% amorphous matter, 11% phytoplankton, and 2% zooplankton. These average estimates are similar to our results for fish from randomly selected creeks (81% amorphous matter, 17% phytoplankton, and 1% zooplankton; Table 1). Although bacteria have been considered to be a possible source of nitrogen (Peters and Kjelson 1975) and a major constituent of amorphous matter in the diet (Peck 1894), the consistently low representation of bacteria (less than 1% of the stomach contents) indicates they are probably not a major source of protein or energy. The low abundance of recognizable plant fragments in the stomachs indicates that such detrital particles are not a major food of Atlantic menhaden.

June and Carlson (1971) based their speculations that amorphous matter in the stomachs of fish was ruptured flagellates on similarities in the appearance of that material and flagellated organisms from the local environment. However, flagellates often account for a small percentage of the phytoplankton—only about 1% in the study of June and Carlson (1971)—and phytoplankton typically account for a small percent of the seston (Riley 1970; Campbell and Spinrad 1987). Thus, unless flagellates are eaten selectively, it is unlikely that they account for most of the amorphous matter in the stomachs of Atlantic menhaden. We are unaware of any evidence that suggests this degree of feeding selectivity and believe that it is unlikely that the amorphous matter in the stomachs of the fish we sampled was ingested as flagellated organisms.

Chemical evidence also indicates that amorphous matter in the stomachs of the fish we examined was not ingested as living matter. If amorphous matter were the residuum of fragile flagellates, its chemical composition (Table 3) would be similar to the chemical composition reported for those organisms. However, the ash content (70% dry weight) of stomach contents that were largely composed of amorphous matter was considerably higher than the ash content of dinoflagellates (11% dry weight: Parsons et al. 1961); its carbohydrate content (14% AFDW) was lower than would be expected (38% AFDW: Parsons et

TABLE 2.—Concentrations of carbohydrates, humic compounds, and ash in the stomach contents of juvenile and adult Atlantic menhaden from estuarine and coastal waters of the east coast of the United States, 1985–1986.

Sample area	Statistic[a]	Carbo-hydrates (% ash-free dry weight)	Humic com-pounds (% ash-free dry weight)	Ash (% dry weight)
Randomly selected creeks				
All	Mean	16.7	37.5	70.2
	SE	0.9	2.2	1.8
	CV	26.4	30.0	13.0
	N	20	20	20
Seasonally sampled creeks, North Carolina				
Pungo Creek	Mean	12.0	27.9	56.9
	SE	1.4	4.8	5.7
	CV	26.4	26.4	22.5
	N	5	5	5
Broad Creek	Mean	8.9	34.2	60.8
	SE	0.5	2.8	1.9
	CV	14.6	23.0	8.8
	N	8	8	8
Coastal waters				
All	Mean	15.1	22.9	58.4
	SE	2.7	2.7	6.2
	CV	50.5	33.2	30.1
	N	6	6	6

[a] CV = coefficient of variation (100·SD/mean). N = number of stomachs.

al. 1961); and its humic content (38% AFDW) was much too high, because such material is virtually absent in living organisms. The high ash content of this material indicates that it is probably not the residue of fragile organisms, and its humic content indicates that it was probably not the residue of living organisms. Although the estimated concentrations of these compounds differ from flagellate chemical composition, they were similar to values reported for amorphous aggregates: ash, 55–80% dry weight (Odum and de la Cruz 1967; Alldredge 1979; Bowen 1979; Romankevich 1984); carbohydrates, 17–24% (Alldredge 1979;

TABLE 3.—Concentrations of carbohydrates, humic compounds, and ash in 14 Atlantic menhaden stomachs that contained 86–96% amorphous matter.

Statistic	Carbohydrates (% ash-free dry weight)	Humic compounds (% ash-free dry weight)	Ash (% dry weight)
Mean	14.4	38.1	70.5
SE	1.1	3.0	2.4
CV[a]	27.5	29.1	12.8

[a] CV = coefficient of variation (100·SD/mean).

Bowen 1979); and humic compounds, about 50% AFDW (Romankevich 1984). Because the chemical composition of amorphous matter in the stomachs is vastly different from the chemical composition of living organisms but similar to that reported for amorphous aggregates, we conclude that the amorphous material in the stomachs was ingested in that form.

Although the relative abundance of zooplankton in the diet of fish from Broad Creek is moderately high, we believe this is atypical of estuarine creeks. Several observations support this conclusion: (1) the average for fish from Broad Creek (24.8%) was substantially higher than the average for fish from any of the randomly selected estuarine creeks (1.1%); (2) the average in nearby Pungo Creek was also much lower (3.7%); and (3) the average from Broad Creek in this study was much higher than the average (0.16%) reported for the same creek during the same time of year by Lewis and Peters (1984).

The difference in relative amounts of amorphous matter in stomachs of fish collected from estuarine and coastal habitats (Table 1) may reflect its abundance in those areas. Peck (1894) concluded that the relative abundance of items in the diet was strongly related to their availability. We did not determine the availability of the various dietary items in the sampling areas, but the lower relative abundance of amorphous matter in the diet of fish from coastal waters probably reflects its lower relative abundance in coastal waters. The higher concentrations of amorphous aggregates in estuarine habitats, may result from higher flocculation of particulate matter, sediment loading, particle resuspension, and lower settling rate of particles because of constant mixing (Carriker 1967).

On the basis of the primary literature and the results of our study, we conclude that amorphous aggregates may be a potentially important nutritional resource for Atlantic menhaden. Our data clearly indicate that amorphous matter is the largest component of the diet of Atlantic menhaden in both estuarine habitats and coastal habitats; with plankton relatively more abundant in coastal areas. Although amorphous aggregates are generally more nutritionally available than detritus formed by fragmentation (Camilleri and Ribi 1986; Bowen 1987; Mann 1988), the contribution of amorphous aggregates to the nutrition of Atlantic menhaden remains unquantified.

Our finding that amorphous matter is the primary component of the stomach contents of At-

lantic menhaden in estuarine creeks poses an interesting challenge to the management of coastal resources. The relative contributions of vascular plants, phytoplankton, and edaphic and epiphytic microalgae to the dissolved organic pool from which this amorphous matter in the diet of Atlantic menhaden seems to be derived are not well defined. Therefore, the trophic links between primary producers and fisheries species are uncertain. To improve our model of energy flow in estuarine and coastal ecosystems and to facilitate management of those habitats, it may be necessary to determine the relative contributions of different plant sources to the dissolved organic matter pools from which amorphous aggregates are formed.

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